Predation Risk and Avoidance Behavior in Two Freshwater Snails

JAMES E. ALEXANDER, JR.[1] AND ALAN P. COVICH

Department of Zoology, University of Oklahoma, Norman, Oklahoma 73019

Abstract. We examined the predator avoidance behaviors of two common freshwater snails, *Physella virgata* and *Planorbella trivolvis,* to the crayfish *Procambarus simulans.* In response to crayfish predation, the snails crawled above the waterline for several hours, then returned to the water. A significant size-dependent relationship existed between crawlout (vertical migration above the waterline) and vulnerability to predation. All observed size classes of *P. virgata,* and small *P. trivolvis,* were vulnerable and crawled out in response to crayfish predation. Large, invulnerable *P. trivolvis* did not display any overt avoidance behavior, but relied instead on strong shell architecture for defense. We suggest that, in these species, crawling above the waterline reduces the probability of an encounter between vulnerable thin-shelled snails and crayfish. This behavior is an adaptive response to predation.

Introduction

Predation is an important cause of evolutionary change in many prey taxa (Vermeij and Covich, 1978; Vermeij, 1982a, b). Predators influence their prey populations in various ways; one aspect of predation in freshwater systems that is receiving increasing attention is the behavioral interactions that occur between predator and prey (Peckarsky, 1984; Sih, 1984). The relative impact of invertebrate predators on freshwater snails, and the responses of the snails to their predators have frequently been studied (Townsend and McCarthy, 1980; Covich, 1981; Brown and DeVries, 1985; Lodge *et al.,* 1987; Brown and Strouse,

1988; Crowl and Covich, 1990; Crowl, 1990; Hanson *et al.,* 1990; Kesler and Munns, 1990; Alexander and Covich, 1991). Freshwater snails exhibit predator avoidance mechanisms, such as burying into substrata, and crawling into vegetation or above the waterline (Snyder, 1967; Townsend and McCarthy, 1980; Alexander and Covich, 1991).

Comparative studies on a variety of animals have shown that closely related or co-occurring species may respond differently to a predator. In other situations, juveniles or smaller individuals that are vulnerable to predators show stronger antipredator responses than larger, older, or other, relatively less vulnerable prey (Stein, 1977; Schmitt, 1982; Sih, 1982, 1986; Werner and Hall, 1988). In these studies, prey appear to assess the tradeoffs between predation risk and foraging for food; *i.e.,* the vulnerable species or size classes forage in different habitats, or at different times, than the invulnerable prey. Comparative studies, by revealing the variety and relative effectiveness of antipredator responses, help to elucidate the adaptive nature of a response. In this paper, we describe the predator avoidance response of two common, co-occurring freshwater snail species, *Physella virgata* (Pulmonata, Physidae, Fig. 1A) and *Planorbella trivolvis* (Pulmonata, Planorbidae, Fig. 1B, C), to their predator, the crayfish *Procambarus simulans* (Decapoda, Astacidae). In another paper (Alexander and Covich, 1991), we demonstrated that *Physella virgata* performs a chemically mediated predator avoidance behavior (crawling above the waterline for a minimum of 2 h) in response to an actively foraging crayfish predator. *Physella virgata* appears to react to chemicals emanating from crayfish and from injured conspecifics. In this study, we demonstrate a size-dependent avoidance response that corresponds to the relative vulnerability of a snail to crayfish predation.
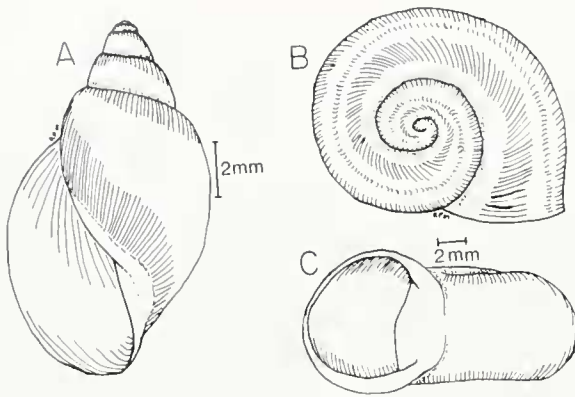
Figure 1. The shell morphology of *Physella virgata* (A) and *Planorbella trivolvis* (B and C). The size bar is 2 mm.

Materials and Methods

Study site and general methods

The snails and crayfish used in this study were collected from Oliver Wildlife Preserve (Norman, Oklahoma). Oliver Wildlife Preserve is a forested area on the South Canadian River floodplain that is inundated periodically by runoff and heavy spring rains. The middle third of the preserve typically remains under water throughout the late winter to early summer months (December to June) and supports large populations of *P. virgata*, *P. trivolvis*, and *P. simulans* (Alexander, 1987). Woody debris in Oliver Wildlife Preserve provide abundant substrata onto which the snails migrate to avoid predators; snails were observed above the waterline throughout the year at Oliver Wildlife Preserve and at other sites (pers. obs.).

Laboratory experiments were conducted at night, in darkness, simulating the natural conditions under which crayfish are most active. No substratum was included in these experiments. For the handling time and ingestion probability experiments (Experiment 1), where crayfish and snails were under continuous observation, low intensity red light was used to facilitate observations. In the second experiment, low intensity white light was used briefly to record observations. When not used in experiments, snails were maintained in 40–80-l aquaria and fed commercial fish food (TetraMin) and lettuce *ad libitum*. Crayfish were housed individually in 4-l plastic containers and fed fish food pellets and lettuce *ad libitum*. Crayfish were starved for at least 24 h prior to the start of the experiments.

Experiment 1: differential vulnerability of Physella *and* Planorbella

This experiment was aimed at examining the ability of *P. simulans* to handle and ingest different size classes of *P. virgata* and *P. trivolvis*. A 10-l aquarium was placed so that the actions of the crayfish and snails could be observed under low intensity red light illumination, regardless of their position in the aquarium. The snails were sorted according to shell length (SL), in 1-mm increments (±0.5 mm), ranging from 5 to 12 mm. For each observation, 50 snails of one size class and species were placed in the aquarium in 2 l of previously aerated tap water. One adult *P. simulans* [carapace length (CL) = 28–36 mm] was then added to the aquarium. Two variables were recorded during the observation period: (a) handling times (time spent consuming a prey), and (b) ingestion probabilities (if a snail was eaten, rejected, or had escaped from the predator once captured). The crayfish (n = 6) were tested with all size classes of both species, randomly, during 15-min observation times, over a 2-week period. Crayfish were observed feeding on one size class of one snail species in all observation periods. Handling time was defined as the period including the capture of the snail, the consumption of the snail, the crayfish cleaning its mouthparts, and the movement forward by the crayfish to continue foraging. Each snail capture was noted, as well as the number of snails that were either consumed or rejected. The ratio of number of snails eaten to the number of snails captured was defined as the ingestion probability.

Experiment 2: size-mediated predator avoidance

To examine the relationship between snail size, predation vulnerability, and avoidance behavior in both snail species, *P. virgata* and *P. trivolvis* were sorted into five size categories (4.1–6.0, 6.1–8.0, 8.1–10.0, 10.1–12.0, and 12.1–16.0 mm SL). A total of 100 snails of one species was added to each 40-l aquarium (25 × 50 × 30 cm) with 5 l of previously aerated tap water. Due to unequal numbers available from the field in each size class, the size class categories contained unequal numbers of snails. With *P. virgata*, the numbers of snails per size class added were: 10, 30, 30, 25, and 5 snails in each of the increasing size classes, respectively. With *P. trivolvis*, the numbers of snails per size class were: 30, 30, 20, 10, and 10 snails in each of the increasing size classes, respectively.

To half of the eight replicates per snail species, one adult (CL = 30–40 mm) *P. simulans* was added at 2200 h. The other four replicates served as predator-free controls. The crayfish were allowed to feed without interruption for 2 h in total darkness, then the number of snails out above the waterline, as well as the number of snails eaten, were determined for each size class and species. Because all five snail class sizes were included in each aquarium, a split-plot ANOVA examined the effects of the two independent variables (presence or absence of crayfish and snail size) on the number of snails killed in

each size class (dependent variable). A second ANOVA separately analyzed differences in the number of surviving snails in each size class found above the waterline as the dependent variable. Each snail species was analyzed separately. Because the data were expressed as proportions (proportion of the snails killed and the proportion of the surviving snails above waterline), the data were arc-sine transformed prior to analysis (Sokal and Rohlf, 1981).

Results

Experiment 1: differential vulnerability of Physella and Planorbella

Handling times increased exponentially with increasing snail size for both species (Fig. 2A). For *P. trivolvis,* handling times increased more rapidly with increasing shell size than did the handling times for *P. virgata.* For each snail prey, an exponential equation was fitted by least squares non-linear regression to the handling time data of each snail species. The resultant best-fit non-linear regression between shell length (SL) and handling times (HT) for *P. virgata* was $HT = 0.095 \ e^{0.28(SL)}$ (n = 279, r^2 = 0.75), and for *P. trivolvis:* $HT = 0.118 \ e^{0.42(SL)}$ (n = 113, r^2 = 0.74). For both species, the best-fit exponential equations fit the data well, explaining 74–75% of the observed variance in the samples.

The ingestion probabilities decreased more rapidly with increasing shell size for *P. trivolvis* than for *P. virgata* (Fig. 2). Approximately 60% of the smallest *P. trivolvis* (5–7 mm SL) were not eaten once captured, and few of the larger *P. trivolvis* (>8 mm SL) were picked up by the crayfish. In contrast, all small *P. virgata* (<8 mm SL) were eaten, once captured. The difference in vulnerability between the two snail species was significant; *P. virgata* were more likely to be eaten, once captured, at all size classes (Wilcoxin signed-ranks test, T = 0, n = 5, P < 0.05, Siegel, 1956). The snail size at which 50% of prey captured were rejected (called R^{50}) was calculated from linear regression analyses run for each individual crayfish, using the rejection data (log 10 transformed). The mean R^{50} for *P. trivolvis* was 6.5 mm, and the mean R^{50} for *P. virgata* was 10.7 mm. The R^{50} for *P. trivolvis* was larger than the R^{50} for *P. virgata* for each crayfish used in the experiment (Wilcoxin signed-ranks test, T = 0, n = 6, P < 0.05).

For both prey species, handling times decreased at the largest size class tested. The apparent decrease occurred because the three smaller crayfish used in the study could not consume snails greater than 8 mm SL (in *P. trivolvis*) and 12 mm SL (in *P. virgata*).

Experiment 2: size-mediated predator avoidance

Two-way analysis of variance results demonstrated that in *P. virgata,* only the presence of a predator had a sig-
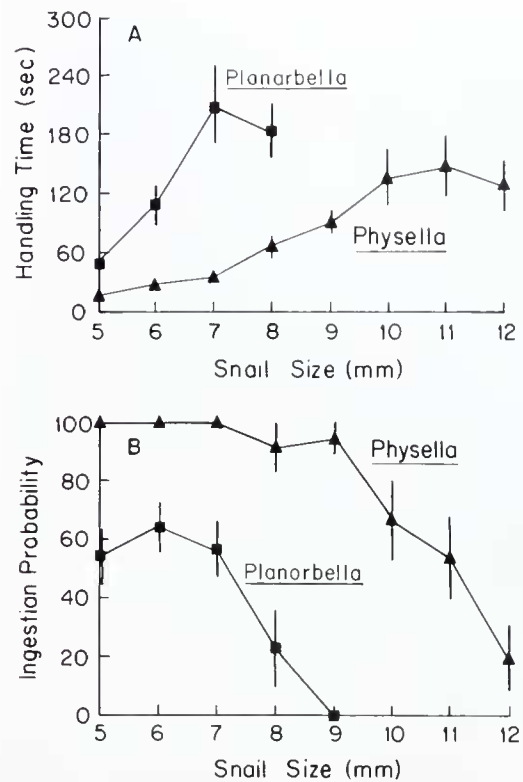

Figure 2. The influence of snail size (shell length) on handling times (A) and ingestion probabilities (B) in *Physella virgata* and *Planorbella trivolvis,* fed upon by *Procambarus simulans.* The error bars are standard errors of the mean.

nificant effect on both dependent variables (the numbers of surviving snails above the waterline and the number of snails killed) (Fig. 3A, B, Table I). No significant effect of snail size was observed in *P. virgata;* all sizes of *P. virgata* were equally vulnerable and were equally likely to crawl above the waterline. In contrast, for *P. trivolvis,* both independent variables (predator presence, snail size) and the interaction between predator presence and snail size all were very significant (Fig. 4A, B, Table 1). The significant size effect was due to the inverse relationship between size and both snail mortality and the number of surviving snails above the waterline. Smaller *P. trivolvis* were more likely than larger individuals to be eaten. In addition to being more vulnerable to *P. simulans* predation, small (4–6 mm SL) *P. trivolvis* displayed the most prominent crawlout response, with most of the surviving snails above the waterline. Medium-sized specimens (6–12 mm SL) of *P. trivolvis* were intermediate in vulnerability and were less likely than smaller animals to display the crawlout response. Larger (12–16 mm SL) specimens of *P. trivolvis* were least vulnerable and did not display an increase in crawlout response over that seen in predator-free control aquaria. No significant level of mortality
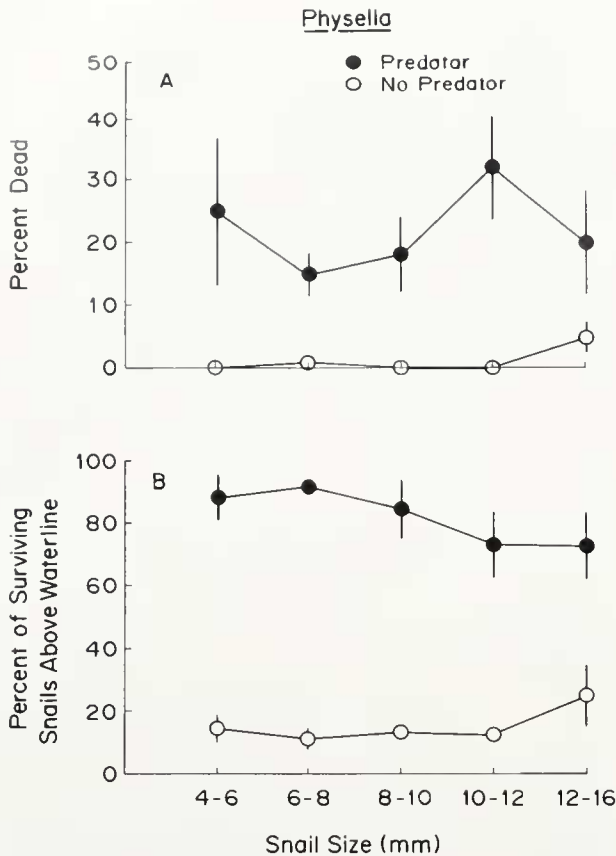
Physella

Figure 3. Size-mediated predator avoidance and death in *Physella virgata*. The upper figure (A) is the percentage of dead snails in each size class (shell length), the lower figure (B) represents the percentage of surviving snails in each size class above the waterline, in both predator (darkened circles) and predator-free control (open circles) treatments (n = 4 in both treatments). The error bars are standard errors of the mean.

Table I

The influence of snail size on crawlout behavior in Physella virgata *and* Planorbella trivolvis

Factor (d.f.)	Variable: % dead		Variable: % crawlout	
	P. trivolvis F	*P. virgata* F	*P. trivolvis* F	*P. virgata* F
Predator presence (1, 6)	119.3***	18.8**	160.5***	146.5***
Snail size (4, 24)	3.0*	0.4	15.5***	0.3
Predator × Size (4, 24)	3.8*	1.0	12.7***	0.7

The table describes the summary of the ANOVA analyses. Each of the dependent variables (percent dead, percent surviving snails above the waterline) were analyzed separately, for each species. (Significance levels are as follows: *$P < 0.05$; **$P < 0.01$; and ***$P < 0.001$.)

(85) among the four replicates in each treatment, suggesting that there was no difference in hunger motivation in the predators used. On average, each crayfish consumed
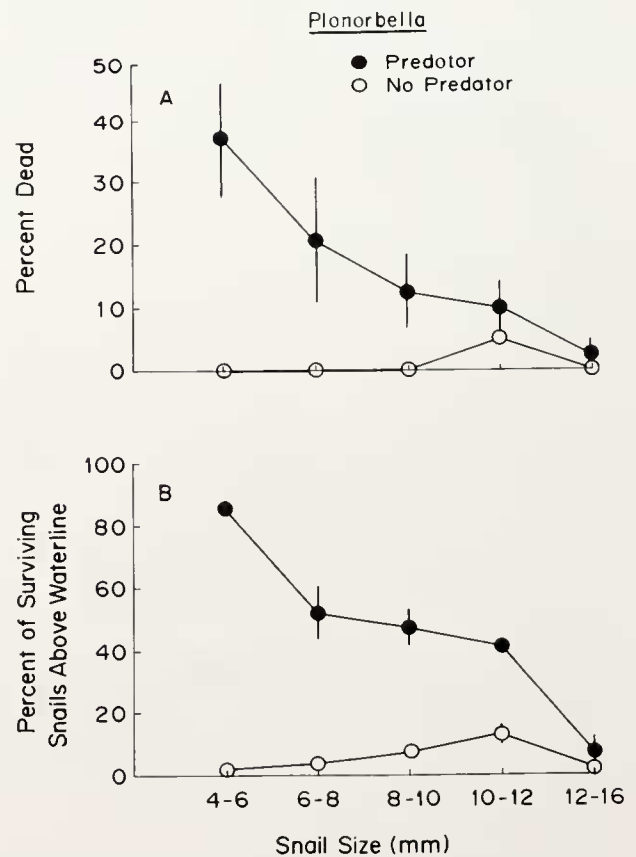
Planorbella

Figure 4. Size-mediated predator avoidance and death in *Planorbella trivolvis*. The treatments and symbols are the same as in Figure 3.

or crawlout was observed in the predator-free control aquaria in either species.

Of the 315 surviving *P. trivolvis*, 23 (7.3%) had some shell damage due to crayfish. The damaged shells were not randomly distributed among the size classes. In the two largest size classes, 8.3% and 5.1% of the surviving 10–12 mm and 12–16 mm SL size classes were damaged, respectively. The two smallest (4–6 mm and 6–8 mm SL) size classes had fewer damaged shells than expected (1.3% and 6.3%, respectively), based on the number of snails originally available in each size class, while the intermediate (8–10 mm SL) sized class had more damaged shells than expected, 15.7% (χ^2 goodness-of-fit test, $\chi^2 = 10.9$, d.f. = 4, $P < 0.05$). In marked contrast, only one out of the 314 surviving *P. virgata* (in the 8–10 mm SL size class) showed shell damage due to crayfish manipulation.

There was no difference in the predation intensity in aquaria housing *P. trivolvis* or *P. virgata;* the crayfish consumed equal numbers of *P. virgata* (86) and *P. trivolvis*

slightly more than 21 snails of either prey species during the 2-h observation period.

Discussion

In marine systems, gastropod anti-predator structures and behaviors are common. Marine snails rely either on strong shell architecture (Palmer, 1979; Bertness *et al.*, 1981; Schmitt, 1982; Blundon and Vermeij, 1983; Lowell, 1986) or on escape and avoidance behavior. Many marine snails crawl towards or above the waterline to temporarily escape from or avoid their predators, such as crabs, sea stars, and predatory gastropods (Feder, 1963; Ansell, 1969; Phillips, 1976; Vaughn and Fisher, 1988). Like many marine gastropod species, the crawlout responses in *P. virgata* and *P. trivolvis* represent the active use of a potential refuge (the terrestrial environment) that temporarily protects these freshwater snails from crayfish predation.

In this study, handling times (time spent consuming prey) and the ingestion probabilities (probability of consuming a prey) were expected to differ between the two prey, because differences in vulnerability existed due to differences in relative shell thickness and shell shape between the two snail species. From these results, it was clear that *P. virgata* were much more vulnerable to crayfish than similar-sized *P. trivolvis.* Crayfish could not consume large *P. trivolvis,* because they could not either crush the thicker planispiral shell or manipulate the shell to a position where the mouthparts could crush it or chip the thickened aperture lip (pers. obs.). Crayfish often dropped large *P. trivolvis* (SL > 6 mm) after lengthy handling periods, and subsequently ignored large *P. trivolvis* after several unsuccessful predation attempts. In contrast, in all size classes, the thinner, elongated spiral shell of *P. virgata* could be manipulated and crushed by the same crayfish, strongly suggesting that specimens of *P. virgata* were more vulnerable to crayfish predation than *P. trivolvis.* Crayfish either crushed the shell at the body whorl, chipped away at the aperture lip, or had broken off the shell spire (pers. obs.). Because their shells provided little structural defense, specimens of all size classes of *P. virgata* were equally vulnerable to crayfish predation and thus were equally likely to crawl above the waterline (Fig. 3).

In examining the surviving snails from the second experiment, only one living specimen of *P. virgata* with a damaged shell was observed in the experiment, strong indirect evidence that, once a specimen of *P. virgata* was captured, the snail was usually eaten. In addition, when foraging on *P. virgata,* crayfish almost always were able to effectively handle and consume *P. virgata* encountered, as shown by the high ingestion probabilities (Fig. 2). For *P. trivolvis,* 23 (7.3%) of the surviving animals recovered in the second experiment were observed with some dam-

age, suggesting that they survived a predatory encounter with the crayfish.

At any given size, specimens of *P. trivolvis* required 2–4 times the handling time by crayfish for successful predation than did similar-sized *P. virgata* (Fig. 2A), indicating the much greater difficulty in crushing the *P. trivolvis* shells. Stein *et al.* (1984), comparing the prey value of a physid (*Physa* sp.) and a planorbid (*Helisoma* sp.) to redear sunfish (*Lepomis microlophus*), noted that redear sunfish weakly selected the physid over the planorbid, but that size selection did not occur within either genus. The force required to crush the physid (3 Newtons for 10 mm SL *Physa* lying aperture down) was less than that required to crush the planorbid (4 Newtons for 10 mm SL *Helisoma* lying on its side), but the difference in force was not dramatically different. The shells were crushed in this way because sunfish were observed orienting snails between their pharyngeal gill plates (their crushing surfaces) so as to crush the minimal dimension of the shell. Crayfish in our study crushed snail shells primarily by chipping with their mandibles at the shell aperture, holding the snail with their maxillipeds. Sometimes, crayfish appeared to use their chelae to balance and press the shell against their mandibles. Although we did not measure the force required for crayfish to crush *P. virgata* and *P. trivolvis* shells, nor did we measure the shell thicknesses, the data suggest that crayfish could more easily crush *P. virgata* shells than *P. trivolvis* shells, because crayfish primarily attempt to break the aperture lip, particularly in *P. trivolvis,* and not the entire shell.

Antipredator mechanisms may be quite dissimilar in closely related gastropod species. Two congeneric species of marine snails, *Tegula eiseni* and *T. aureotincta,* differ in their predator defenses; *T. aureotincta* performed avoidance behaviors to gastropod and asteroid predators, while *T. eiseni* depended more on shell morphology for defense (Schmitt, 1982). *Physella virgata* relies on behavioral avoidance much more exclusively than does *P. trivolvis,* which appears to rely more on predator avoidance when young, and on shell strength as larger adults.

The correspondence between the reactivity of snails of a given size class and their vulnerability was expected, if predator avoidance behavior (crawlout) has some costs associated with reacting inappropriately to the potential threat of predation. Crawling to or above the waterline could expose the snail to other predators, including birds, and certain insects, such as belostomatids (Crowl and Alexander, 1989; Kesler and Munns, 1990). Further costs to crawlout behavior include decreased foraging time (if the animals cannot forage on food above the waterline), decreased opportunities for reproduction, and desiccation (Alexander and Covich, 1991).

The differences in the antipredator responses between the two species may be influenced by differences in selective pressures caused by the distinct physiological adaptations used by the two snails in their respective microhabitats (McMahon, 1983). *Planorbella trivolvis,* with its well-developed neomorphic gill, and its more efficient respiratory pigment (hemoglobin), is much more aquatic than *P. virgata,* which retains an air-filled mantle cavity (lung) as the major organ of gas exchange. *Physella virgata* makes periodic excursions to the surface to renew its oxygen store, and subsequently is limited to shallow water near-shore habitats or those habitats with structure (*i.e.,* aquatic macrophytes or woody debris) extending above the waterline. *Planorbella trivolvis,* with a much greater capacity for aquatic gas exchange, makes excursions into much deeper water, where crawlout sites are likely to be unavailable. In *P. virgata,* physiologically restricted to shallow, near-shore waters, selective pressures may have caused a retention of a strong crawlout response to avoid predators and reduced pressure for the development of a structurally predator-resistant shell. In contrast, *P. trivolvis,* whose range (particularly in adults) extends into deeper water and consequently has little access to terrestrial refugia, selection pressures may have been towards development of a structurally predator-resistant shell and a reduced dependence on a crawlout response.

Because they can be the dominant primary consumers in some habitats, mollusks and decapod crustaceans play important roles in many aquatic communities. Many are herbivorous, detritivorous, or omnivorous, and are important for cycling nutrients and providing energy in the form of variously sized food items for higher trophic level consumers (Ansell, 1969; Momot *et al.,* 1978; Grimm, 1988). The study of the behavioral interplay between freshwater snails and crayfish is essential in understanding how these behavioral processes influence predator-prey dynamics and community composition. Rapid snail escape and avoidance behavior, and the subsequent decrease in encounter probabilities, suggest that in some structurally complex habitats, such as macrophyte-dominated littoral zones or forested wetland areas, vertical migration above the waterline is an adaptive response to crayfish predation.

Acknowledgments

Literature Cited

Alexander, J. E., Jr. 1987. Predator-prey interactions between freshwater snails and crayfish. Ph.D. dissertation, University of Oklahoma.

Alexander, J. E., Jr., and A. P. Covich. 1991. Predator avoidance in the freshwater snail *Physella virgata* to the crayfish *Procambarus simulans. Oecologia* (in press).

Ansell, A. D. 1969. Defensive adaptations to predation in the mollusca. *Proc. Mar. Biol. Assoc. India Symp. Ser.* **3**: 487–512.

Bertness, M. D., S. D. Garrity, and S. C. Levings. 1981. Predation pressure and gastropod foraging: a tropical-temperate comparison. *Evolution* **35**: 995–1007.

Blundon, J. A., and G. J. Vermeij. 1983. Effect of shell repair on shell strength in the gastropod *Littorina irrorata. Mar. Biol.* **76**: 41–45.

Brown, K. M., and D. R. DeVries. 1985. Predation and the distribution and abundance of a pulmonate pond snail. *Oecologia* **66**: 93–99.

Brown, K. M., and B. H. Strouse. 1988. Relative vulnerability of six freshwater gastropods to the leech *Nephelopsis obscura* (Verrill). *Freshwater Biol.* **19**: 157–165.

Covich, A. P. 1981. Chemical refugia from predation for thin-shelled gastropods in a sulfide-enriched stream. *Verh. Int. Vereinigung Theoret. Angewandte Limnol.* **21**: 1632–1636.

Crowl, T. A. 1990. Life-history strategies of a freshwater snail in response to stream permanence and predation: balancing conflicting demands. *Oecologia* **84**: 238–243.

Crowl, T. A., and J. E. Alexander, Jr. 1989. Parental care and foraging ability in male waterbugs (*Belostoma flumineum*). *Can. J. Zool.* **67**: 513–515.

Crowl, T. A., and A. P. Covich. 1990. Predator-induced life-history shifts in a freshwater snail. *Science* **247**: 949–951.

Feder, H. M. 1963. Gastropod defensive responses and their effectiveness in reducing predation by starfishes. *Ecology* **44**: 505–512.

Grimm, N. B. 1988. Role of macroinvertebrates in nitrogen dynamics of a desert stream. *Ecology* **69**: 1884–1893.

Hanson, J. M., P. A. Chambers, and E. E. Prepas. 1990. Selective foraging by the crayfish *Orconectes virilis* and its impact on macroinvertebrates. *Freshwater Biol.* **24**: 69–80.

Kesler, D. K., and W. R. Munns, Jr. 1990. Predation by *Belostoma flumineum* (Hemiptera): an important cause of mortality in freshwater snails. *J. N. Am. Benthol. Soc.* **8**: 342–350.

Lodge, D. M., K. M. Brown, S. P. Klosiewski, R. A. Stein, A. P. Covich, B. K. Leathers, and C. Bronmark. 1987. Distribution of freshwater snails: spatial scale and the relative importance of physicochemical and biotic factors. *Am. Malacol. Union* **5**: 73–84.

Lowell, R. B. 1986. Crab predation on limpets: predator behavior and defensive features of the shell morphology of the prey. *Biol. Bull.* **171**: 577–596.

McMahon, R. F. 1983. Physiological ecology of freshwater pulmonates. Pp. 359–430 in *The Mollusca, Vol. 6, Ecology,* W. D. Russell-Hunter, ed. Academic Press, Inc., Orlando, FL.

Momot, W. T., H. Gowing, and P. D. Jones. 1978. The dynamics of crayfish and their role in ecosystems. *Am. Midl. Nat.* **99**: 10–35.

Palmer, A. R. 1979. Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. *Evolution* **33**: 697–713.

Peckarsky, B. L. 1984. Predator-prey interactions among aquatic insects. Pp. 196–254 in *The Ecology of Aquatic Insects,* V. H. Resh and D. M. Rosenberg, eds. Praeger Scientific, New York.

Phillips, D. W. 1976. The effect of a species-specific avoidance response to predatory starfish on the intertidal distribution of two gastropods. *Oecologia* 23: 83–94.

Schmitt, R. J. 1982. Consequences of dissimilar defenses against predation in a subtidal marine community. *Ecology* 63: 1588–1601.

Siegel, S. 1956. *Nonparametric Statistics For The Behavioral Sciences* McGraw-Hill, Inc., New York.

Sih, A. 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni. Ecology* 63: 786–796.

Sih, A. 1984. The behavioral response race between predator and prey. *Am Nat.* 123: 143–150.

Sih, A. 1986. Antipredator responses and the perception of danger by mosquito larvae. *Ecology* 67: 434–441.

Snyder, N. F. R. 1967. An alarm reaction of aquatic gastropods to intraspecific extract. *Cornell University Agricultural Experimental Station Memoir* 403.

Sokal, R. R., and F. J. Rohlf. 1981. *Biometry,* 2nd ed. W. W. Freeman and Co., San Francisco.

Stein, R. A. 1977. Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. *Ecology* 58: 1237–1253.

Stein, R. A., C. G. Goodman, and E. A. Marschall. 1984. Using time and energetic measures of cost in estimating prey value for fish predators. *Ecology* 65: 702–715.

Townsend, C. R., and T. K. McCarthy. 1980. On the defence strategy of *Physa fontinalis* (L.), a freshwater pulmonate snail. *Oecologia* 46: 75–79.

Vaughn, C. C., and F. M. Fisher. 1988. Vertical migration as a refuge from predation in intertidal marsh snails: a field test. *J. Exp. Mar Biol. Ecol.* 123: 163–176.

Vermeij, G. J. 1982a. Phenotypic evolution in a poorly dispersing snail after arrival of a predator. *Nature* 299: 349–350.

Vermeij, G. J. 1982b. Unsuccessful predation and evolution. *Am. Nat.* 120: 701–720.

Vermeij, G. J., and A. P. Covich. 1978. Coevolution of freshwater gastropods and their predators. *Am. Nat.* 112: 833–843.

Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology* 69: 1352–1366.